

Movement and Space Use by Coastal Rosy Boas (*Lichanura trivirgata roseofusca*) in Coastal Southern California

JAMES E. DIFFENDORFER,^{1,2} CARLTON ROCHESTER,^{3,4}
ROBERT N. FISHER,^{3,5} AND TRACEY K. BROWN^{6,7}

¹Department of Biology, San Diego State University, San Diego, CA 92182, USA

³United States Geological Service San Diego Field Station, 5745 Kearny Villa Road, Suite M,
San Diego, California 92123, USA

⁶Applied Conservation Division, Zoological Society of San Diego, P.O. Box 120551,
San Diego, California 92112 USA

ABSTRACT.—We studied the movement ecology of Coastal Rosy Boas (*Lichanura roseofusca*) by radio tracking 17 animals across four sites for up to four years. The typical movement pattern included many short distance moves with rare long distance movements. These skewed distributions made the mean a poor descriptor of movement and this is likely a common issue in other studies. Sexes had similar movement patterns and moved less frequently and shorter distances per day during cooler seasons. Rare long-distance movements occurred primarily in the spring. Propensity to move and mean distance moved per day varied across sites. Home-range size increased with additional fixes even after four years and had a seasonal pattern, increasing during warmer seasons and remaining stable or shrinking during cooler seasons. Despite using novel habitat in sequential years, nearly all individuals used the same general area over longer periods of time. Finally, individuals of both sexes had high levels of spatial overlap. The results indicate for *L. roseofusca* (1) Individual variability in movement is more the rule than the exception; (2) Common seasonal patterns in movement and space use do exist; (3) Home-range sizes vary through time yet remain in the same general location; and (4) A lack of territoriality and considerable overlap in space use exist.

The spacing of individuals, as well as the frequency and distance of their movements, affects population dynamics. Empirical studies indicate spatial dispersion and movement affect population size and trajectory at multiple scales: from metapopulation dynamics in butterflies (Fahrig and Paloheimo, 1987; Hanski et al., 1995) and salamanders (Trenham et al., 2001), to source-sink dynamics in grasses (Keddy, 1981, 1982; Watkinson et al., 1989), and to ideal free habitat selection in small mammals (Diffendorfer, 1998) and birds (Doncaster et al., 1997).

In addition to affecting population dynamics, dispersion patterns and movement often reflect ecological, behavioral, or social interactions among individuals (Huffaker, 1958; Wynne-Edwards, 1967; Pusey, 1987; Pulliam, 1988; Danielson, 1991, 1992). Thus, natural selection likely has strong impacts on many aspects of movement, ranging from physiological and anatomical adap-

tations enhancing movement ability, to selection for the propensity to disperse (Holt, 2003).

Given difficulties inherent in measuring snake movements and the relatively recent use of radiotelemetry techniques, no general theory of snake movement exists to define explicit, testable hypotheses. Indeed, after reviewing over 50 papers on snake movements, Macartney et al. (1988) suggested the number of variables affecting movement patterns and the lack of specific analyses of movement precluded any general conclusions. Although numerous subsequent studies exist, snake ecologists are still in the formative stages of understanding snake spatial ecology.

Factors affecting snake movement include the particular ectothermic physiology of a species and the need to find locations suitable for thermoregulation (Huey et al., 1989; Dorcas and Peterson, 1998; Whitaker and Shine, 2002; Pringle et al., 2003; Whitaker and Shine, 2003). Many snake species move long distances to and from seasonal hibernacula, returning to specific locations during stressful conditions while foraging elsewhere during favorable conditions. During reproductive activity, a number of studies found increased movement in males, presumably seeking mates (Jenkins et al., 2001). In addition, females often travel to a particular location with a preferred thermal environment and reduce

² Corresponding Author. Present address: Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, USA; E-mail: jdiffer@inhs.uiuc.edu

⁴ E-mail: crochester@usgs.gov

⁵ E-mail: rfisher@usgs.gov

⁷ Present address: Department of Biological Sciences, California State University, San Marcos, San Marcos, California 92096, USA; E-mail: traceyb@csusm.edu

activity when gravid (Brown and Weatherhead, 2000).

In perhaps the most comprehensive review of snake movement ecology, Gregory et al. (1987) suggested the spatial pattern and density of critical resources (hibernacula, ponds, prey, etc.) may best explain major patterns in movement. Gregory et al. (1987) argued snake dispersion should be nonrandom given a lack of evidence for territoriality and given the formation of seasonal or short-term aggregations. Habitat selection for favorable conditions may result in short-term aggregations as snakes thermoregulate or select areas of high prey density (Reinert, 1993; Whitaker and Shine, 2003). Larger, longer-term aggregations may result from mating (Aleksiuk and Gregory, 1974), overwintering (Gregory, 1984), stressful conditions (Aleksiuk, 1977), and communal oviposition or reproduction such as aggregations of gravid females (Duvall et al., 1985).

The Coastal Rosy Boa (*Lichmura trivirgata roseofusca*) is one of two boid species native to the United States (Stebbins, 2003). Until recently, little data existed about spatial ecology, activity patterns or even basic natural history information of rosy boas (Rodriguez-Robles et al., 1999). In an unpublished 1996 report to the Arizona Game and Fish Department, D. A. Parizek, P. C. Rosen, C. R. Schwalbe, and C. H. Lowe provided data on movement, habitat selection, and activity patterns of six rosy boas collected using telemetry. Dorcas (1995) studied the thermal ecology of Rubber Boas (*Charina bottae*), providing detailed information on daily activity patterns and body temperature (Dorcas et al., 1997; Dorcas and Peterson, 1998). Coastal populations of rosy boas exist in a rapidly fragmenting landscape (Hunter et al., 2003), and understanding spatially explicit movements is necessary for evaluating reserve sizes and for long-term management of this species (Case and Fisher, 2001). Here, we extend work on the spatial ecology of rosy boas by analyzing radiotelemetry data from 17 individuals at four sites over four years. We report results related to movement, individual spacing and overlap, and seasonal changes in movement patterns. Data on thermal ecology and habitat selection of rosy boas will be presented in other publications.

MATERIALS AND METHODS

Study Sites.—We began in May 1999 by collecting animals using visual searches, road surveys, and pitfall arrays used in a monitoring project (Fisher and Case, 2000). We added snakes to the study during the first three years, so some individuals were tracked for longer periods than others.

We studied animals at four locations in San Diego and Riverside Counties, all dominated by coastal sage scrub: (1) WAP, San Diego Wild Animal Park, San Diego County, CA (33.09465°N, 116.98253°W, 140–255 m elevation) managed by the Zoological Society; (2) MT, San Diego County Mission Trails Regional Park, San Diego County, CA (32.81066°N and 117.03789°W, 165–215 m elevation); (3) CNM, Cabrillo National Monument, San Diego County, CA (32.66912°N and 117.24107°W, 22–109 m elevation); this single boa, collected by CNM staff, was the only rosy boa observed at CNM despite eight years of reptile and amphibian monitoring (Fisher and Case, 2000; Case and Fisher, 2001) and given a lack of historic observations, was likely a released captive; and (4) SM, Santa Margarita Ecological Reserve, Riverside County, CA (33.45768°N and 117.17044°W, 790–1120 m elevation).

Telemetry.—We used receivers from Wildlife Materials, Inc. (TRX-1000S), AVM Instrument Co. (LA12-Q), Telonics, Inc. (TR-4 and TR-5), and RA-2AK (Telonics, Inc.) directional antennas. To ensure transmitters weighed less than 5% of a snake's body mass (Hardy and Greene, 1999), we used two types of transmitters by Holohil Systems Ltd. Smaller snakes received the SB-2 (5.5 g, 9 × 19 mm), whereas larger snakes received the temperature sensitive SI-2T (9.5g, 10 × 33 mm).

Surgical procedures used throughout the study followed the guidelines described by Reinert and Cundall (1982) and Hardy and Greene (1999) and had approval by the Animal Use Committee of San Diego State University (protocol 99-011F). C. Rochester, and later L. Young, DVM (San Diego Zoo) performed all implants. We released snakes at the site of collection a few days after surgery, as minimizing time in captivity increases postsurgical survival (Hardy and Greene, 1999).

Field Protocols.—Sampling effort varied as snake activity patterns changed seasonally. During the spring and summer, we located individuals two to four times per week but only once or twice a week during winter and fall. We recorded GPS locations directly above the snake (whether above or belowground) with a GPS handheld unit (Garmin 12-XL or Trimble GeoExplorer3, UTM coordinate system, ~1.5 m accuracy).

Statistical Analyses.—We analyzed the data for differences in movement, by sex, season, and site. We defined each season as: Winter (21 December to 20 March), Spring (21 March through 20 June), Summer (21 June to 20 September), and Fall (21 September to 20 December).

We used the Animal Movement extension (Hooge and Eichenlaub, 1997) in ArcView 3.3 to estimate home-range size. For comparison with older studies of snake home-range size, we

calculated 100% minimum convex polygons (MCP) but also calculated kernel home-range (KHR) sizes because these are more accurate estimators of home-range size (Seaman and Powell, 1996). We report both adaptive and fixed kernel estimates but estimated home-range overlap with fixed kernel estimates. For KHR, we used least-squares cross-validation to determine the smoothing factor (Seaman and Powell, 1996; Blundell et al., 2001). For the overlap analyses, we defined each year from 21–20 December and used these data to calculate an annual home range with the area shared by sequential annual home ranges considered overlap.

Because movement data were extremely skewed, we analyzed two components. First, the proportion of fixes resulting in movements addressed the question “what factors affect the chance an animal moves?” Second, we analyzed the distances moved per day, but only when movement occurred, by excluding distances of zero and asked “when animals moved, how far did they move?” We calculated the proportion of possible fixes resulting in moves (“proportional movement”) for each individual then used *t*-tests or ANOVA to test for differences across treatments. Because the accuracy of our GPS unit was ~1.5 m, we considered distances between successive locations greater than 3 m as movement. Because we typically found animals below ground, we do not feel we could appreciably increase the level of spatial accuracy using other techniques.

As recommended by Gregory et al. (1987), we estimated distance moved per day and distance moved per fix. However, we found a strong correlation between these two estimates of movement so we only analyzed movement per day by sex, season, or site.

Distance moved per day can be calculated in two ways. First, dividing the total distance moved by an individual during the entire study by the total number of days produces a single, overall estimate. Second, estimating the distance moved per day across sequential pairs of fixes (distance moved between two fixes divided by the number of days between the fixes) produces a distribution of distances allowing the calculation of mean (typically), median, mode and variance. Both methods occur in the literature, often reported as “average distance moved per day.” However the two methods do not always produce the same estimate. For example, if an animal moved 2, 3, 2, and 1 units in 1, 4, 8, and 2 days, its overall distance/day = $(2 + 3 + 2 + 1) / (1 + 4 + 8 + 2)$ or 8 units/15 days = 0.5333, but the mean distance moved per day equals the mean of $(2/1, 3/4, 2/8, 1/2) = (2 + 0.75 + 0.25 + 0.5)/4 = 0.875$. We advocate estimating sequential distances moved per day and then

using estimators of central tendency, variability, and skewness to describe and compare the distributions.

We estimated sequential movements per day, excluding periods of no movement, then compared it between sexes, sites, or seasons using *t*-tests or ANOVAs. Even after removing distances of zero, the distances moved per day were highly skewed, so we used 4th-root transformations to meet the assumptions of normality.

The data contained high levels of temporal correlation: if an animal moved a short distance in one time period, it likely moved a similar short distance the following time period. To avoid pseudoreplication, we used individuals as replicates. Thus, our statistical tests often compared “means of means” because we averaged movements for an individual within a season, or site, and used individuals as the unit of replication in the appropriate statistical test. Given our opportunistic sampling effort, we did not have adequate sample sizes to statistically analyze all combinations of sex, site, and season. Therefore, we performed less complex one- and two-way analyses when appropriate. Finally, we used correlations to check for relationships between individual body size and distance moved per day.

RESULTS

We captured 25 snakes, implanted transmitters in 21, and obtained sufficient movement data from 17 (Table 1). The fates of implanted animals varied with most surviving during the study. The four unused individuals died, were eaten, or disappeared from the study area before we could gather a sufficient set of fixes (Table 1). We located the 17 snakes 1169 times. As a result of cumulatively adding snakes to the study, implantation dates, total number of days tracked, and total number of locations varied substantially across individuals (Table 1). On average, snakes were located 1.3 times per week. Sampling effort varied by location and by season (Table 2) resulting partly from the closer geographic proximity of WAP and MT.

Proportional Movement.—Males and females had similar proportional movement ($t = -0.268$, $df = 15$, $P = 0.793$, Table 3, column C); thus, we combined data across sexes to investigate seasonal and site effects. Although movement occurred in all months, the probability of an animal moving declined sharply in the winter ($F = 3.567$, $df = 3, 57$, $P = 0.02$, Winter: mean \pm SE = 0.277 ± 0.070 , $N = 13$, Spring: 0.573 ± 0.065 , $N = 15$, Summer: 0.512 ± 0.061 , $N = 17$, Fall: 0.494 ± 0.063 , $N = 16$). At WAP and MT (sites with multiple individuals captured in each season) we performed a two-way ANOVA using site and season as explanatory variables, combining data across sexes. As with the full dataset,

TABLE 1. Summary statistics. ID refers to an individual's identification. Implant date includes recapture and transmitter replacement dates Fate is the disposition of the animal at the end of the study. A = Alive and Active, P = Predated, D = Dead because of complications, U = unknown disposition.

Study site	ID	Sex	Implant date	Days monitored	Number of fixes	Fixes per week	Fate
Cabrillo National Monument (CNM)							
	CNM-1	M	5/99 8/99 5/00	507	65	0.9	A
Mission Trails Regional Park (MT)							
	MT-1	F	7/99	441	76	1.2	A
	MT-2	M	7/99	55	12	1.5	U
	MT-3	F	3/00	216	34	1.1	A
	MT-4	F	3/00	214	35	1.1	A
	MT-5	F	3/00	203	36	1.2	A
Santa Margarita Ecological Reserve (SM)							
	SM-1	F	5/99 4/00	484	81	1.2	A
	SM-2	M	5/99				P
	SM-3	M	5/99				P
Wild Animal Park (WAP)							
	WAP-1	M	5/99 4/00 9/01	1146	162	1.0	A
	WAP-2	M	5/99 5/00	501	108	1.5	A
	WAP-3	M	6/99	214	41	1.3	P
	WAP-4	M	6/99 1/00	485	87	1.2	A
	WAP-6	M	9/99				D
	WAP-7	F	3/00	859	102	0.8	A
	WAP-9	F	4/00	488	70	1.0	A
	WAP-10	M	5/00 9/01	783	81	0.7	A
	WAP-11	F	5/00 10/01	744	81	0.8	A
	WAP-12	F	6/00 10/01	530	62	0.8	A
	WAP-15	M	4/01	428	36	0.6	A

proportional movement showed a trend toward declining in the winter (Season; $F = 2.438$, $df = 3,45$, $P = 0.077$). However, mean proportional movement was higher at WAP (0.517 ± 0.040 , $N = 38$) than at MT (0.327 ± 0.067 , $N = 15$, $F = 8.515$, $df = 1,45$, $P = 0.005$), and this difference did not change with season (Site \times Season; $F = 0.221$, $df = 3,45$, $P = 0.881$).

We compared the single individuals at SMER and CNM to the average proportional movement at both MT and WAP using one-sample t -tests. The male boa at CNM had a higher proportion of fixes that were movements (0.64) than the boas at either WAP (0.52 ± 0.04 , $N = 10$; $t = -2.478$, $df = 9$, $P = 0.035$) or MT (0.29 ± 0.04 , $N = 5$; $t = -5.880$, $df = 4$, $P = 0.004$). The female at SMER had a higher proportion of fixes that were movements (0.56) than the boas at MT ($t = -4.028$, $df = 4$, $P = 0.016$) but not WAP ($t = -0.769$, $df = 9$, $P = 0.462$).

Distances Moved.—Frequent short distance movements and rare, long moves resulted in right skewed distributions of distances moved per day for all individuals across all sites (Fig. 1). Summary statistics for all snakes show how the skewness and the method of calculation influence our perception of snake movement (Table 3). For example, mean distance moved per day and mean distance moved per move were greater than median values in nearly all cases. Given the influence of rare long-distance movements, overall meters moved per day (total m moved/total days) was typically smaller than mean distance moved per day (Table 3, column F vs. column G). We used mean distance moved per day in all other calculations.

Excluding cases of no movement, we found positive correlations between distances moved between fixes and distances moved per day in 12

TABLE 2. Total number of fixes by site, season, and sex. Wild Animal Park had sufficient sampling to investigate sex by season interactions. See Table 1 and text for site abbreviations. The number of individual snakes making up the fixes is shown in parentheses.

Season	Sex	Study site			
		CNM	MT	SM	WAP
Fall	Female	0	16 (4)	10 (1)	50 (4)
	Male	15 (1)	0	0	114 (6)
Winter	Female	0	16 (4)	5 (1)	51 (4)
	Male	8 (1)	0	0	68 (5)
Spring	Female	0	98 (4)	32 (1)	101 (4)
	Male	23 (1)	0	0	152 (5)
Summer	Female	0	51 (4)	33 (1)	108 (4)
	Male	19(1)	12 (1)	0	175 (6)
Total number of snakes		1	5	1	10

of 14 individuals (Table 4). These results indicate when animals moved longer distances, they actually moved farther per day and not that long periods between fixes resulted in long-distance movements. Including distances of zero between fixes increased the correlation coefficients and the

sample sizes, making all correlations statistically significant.

Male and female rosy boas had similar distances moved per day (Table 4), and body size did not affect distances moved per day. Like proportional movement, average distance moved per day declined with cool weather ($F = 3.355$, $df = 3, 53$, $P = 0.026$; Table 4). When considered with the low amounts of proportional movement in the winter, the data show rosy boas not only moved much less frequently but also at slower rates during the Winter.

Long-distance movements occurred predominantly in Spring, with 78 of the 114 farthest 1% of the distances moved per day in the Spring, 28 in the Summer, six in the Fall, and two in the Winter. We found no evidence of sexual bias in these movements with females accounting for 48% (55 of 114) of the long movements.

Home-Range Size and Novel Habitat.—Minimum convex polygons (MCP) and kernel home range (KHR) methods produced different estimates of annual home-range size but showed similar patterns of change with increasing numbers of fixes and with season. Home-range size tended to increase with additional fixes for all individuals (Fig. 2A,B) regardless of home-range

TABLE 3. Summary movement statistics for all individuals, both sexes and each season. Summary statistics in columns G, H, I, and J used the entire history of movements for an individual including movements of zero. Standard errors bound mean values. For those rows with means by sex and season, the values are the averages across individuals and represent untransformed values tested in the ANOVAs. Values in parentheses in the column "Sex" represent sample sizes.

ID	Sex	A	B	C	D	E	F	G	H	I	J
		Observed moves	Possible moves	Proportional movement = A/B	Total meters moved	Days	Meters per day = D/E	Mean meters per day ± SE	Median meters per day	Mean meters per move ± SE	Median meters per move
CNM-1	M	41	64	0.64	2038	507	4.02	6.0 ± 1.3	1.8	31.8 ± 6.5	9.3
MT-1	F	26	75	0.35	802	441	1.82	2.9 ± 1.1	0.0	10.7 ± 2.8	0.0
MT-2	M	4	11	0.36	174	55	3.16	1.9 ± 1.1	0.0	15.8 ± 11.2	0.0
MT-3	F	15	33	0.45	353	216	1.63	2.1 ± 1.1	0.0	10.7 ± 3.5	0.0
MT-4	F	9	34	0.26	313	214	1.46	2.0 ± 0.8	0.0	9.2 ± 3.4	0.0
MT-5	F	18	35	0.51	570	203	2.81	4.8 ± 1.3	0.5	16.2 ± 3.9	1.0
SM-1	F	44	80	0.56	912	484	1.88	3.1 ± 0.7	0.5	11.7 ± 2.2	2.0
WAP-1	M	96	161	0.60	2803	1146	2.45	3.5 ± 0.6	0.8	17.6 ± 2.4	6.0
WAP-2	M	30	107	0.29	921	501	1.84	1.8 ± 0.5	0.0	8.9 ± 2.2	0.0
WAP-3	M	12	40	0.30	190	214	0.89	0.7 ± 0.3	0.0	4.8 ± 2.2	0.0
WAP-4	M	37	86	0.43	770	485	1.59	2.7 ± 0.8	0.0	9.1 ± 1.8	0.0
WAP-7	F	55	101	0.56	1094	859	1.27	1.7 ± 0.3	0.3	11.2 ± 2.0	3.8
WAP-9	F	40	69	0.59	1721	488	3.53	4.7 ± 1.0	1.0	25.3 ± 5.9	4.7
WAP-10	M	50	80	0.63	1162	783	1.48	1.9 ± 0.3	0.4	14.5 ± 2.2	5.3
WAP-11	F	42	80	0.53	1002	744	1.35	1.9 ± 0.5	0.1	12.7 ± 2.4	0.9
WAP-12	F	33	61	0.54	656	530	1.24	1.6 ± 0.4	0.1	10.8 ± 2.5	1.6
WAP-15	M	27	35	0.77	1705	428	3.98	4.1 ± 1.0	1.7	48.7 ± 12.0	15.8
Males	(8)			0.50 ± 0.06				2.8 ± 0.59		34.5 ± 5.7	
Females	(9)			0.48 ± 0.04				2.8 ± 0.41		27.6 ± 2.7	
Fall	(16)			0.49 ± 0.06				10.4 ± 2.3		19.5 ± 2.9	
Winter	(13)			0.28 ± 0.07				8.3 ± 5.3		16.5 ± 5.1	
Spring	(15)			0.57 ± 0.06				22.9 ± 3.8		39.5 ± 5.0	
Summer	(17)			0.51 ± 0.07				16.9 ± 3.2		29.8 ± 4.1	

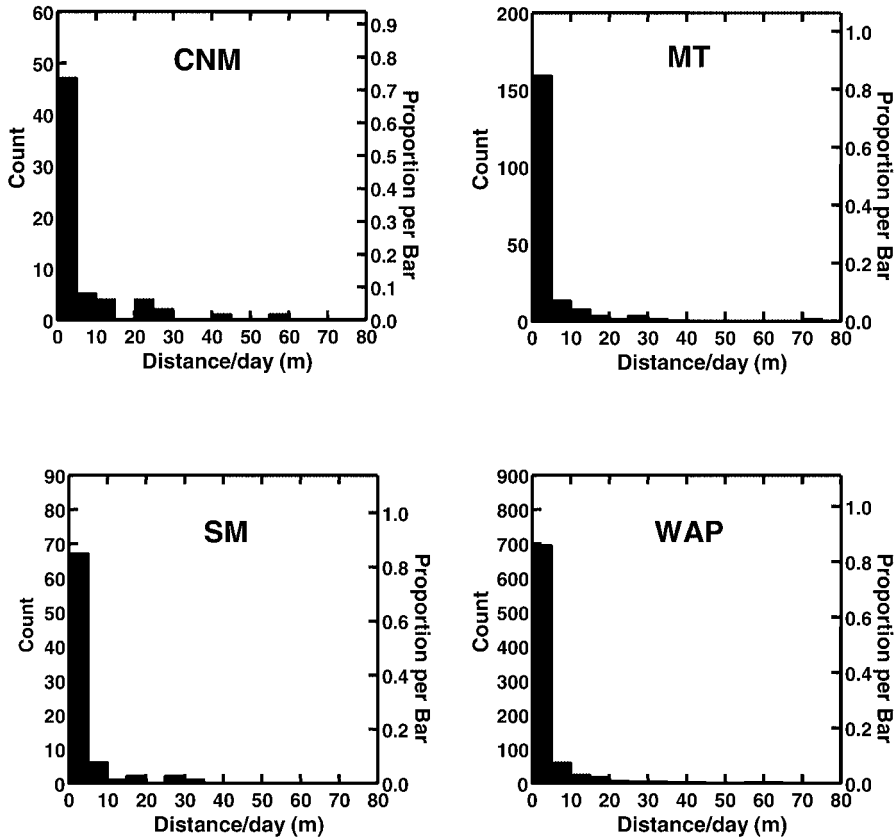


FIG. 1. Frequency histograms of distances moved per day (m) for each of the four study sites. In areas with multiple animals (MT and WAP), data were combined across all individuals resulting in the higher number of total events.

estimator. However, except for the likely released CNM-1, home-range size never exceeded 1.5 ha.

In some cases, the estimate of home-range size declined with additional fixes. Estimators removing a small percentage of the extreme data (95% AK, or FK) sometimes added locations near the center of the home range during periods of no movement, resulting in the removal of outlying points and reductions in home-range size (Fig. 2A). Increases in home-range size typically slowed or stopped during the winter because animals rarely moved (Fig. 2B).

Home-range size increased between years for nine snakes, remained approximately the same for two, and declined for one individual. In some cases, changes were attributed to smaller or larger sample sizes between years, but in general home-range sizes varied between individuals and showed no annual patterns. Given the dynamic nature of home-range size and its dependence on sample size and season of data collection, we did not compare home-range size by sex, season, site, or body size.

In many cases, snakes added considerable amounts of additional area to their home range from one year to the next (mean \pm SE % novel habitat in 2000 = 70.7 ± 13.2 , $N = 6$; 2002 = 73.2 ± 5.1 , $N = 6$; 2003 = 64.6 ± 11.4 , $N = 5$). Despite the addition of habitat, snakes also remained in the same general area over long periods of time reusing substantial areas from previous years. For example, WAP-1 and WAP-10 kept their home ranges in the same general location each year, despite large amounts of novel habitat between years and different directions of change in home range size (WAP-1 decreased, but WAP-10 increased; Fig. 3).

Although we did not quantify home-range overlap, snakes at WAP and MT showed overlap and sympatric space use (Fig. 4). At WAP, 12 snakes (10 radiotracked snakes, and two other small rosy boas) occurred within a 5.6-ha area. There were 26 instances of individual snakes occurring within 5 m of each other. On five occasions, two rosy boas were found together, and in most cases, the two snakes differed in sex.

One pair of snakes (WAP-2, WAP-9), was first found together in March 2001 and again in May 2001. The pair then remained together until mid-June 2001, moving over a 100 m distance.

DISCUSSION

This research highlights four patterns in rosy boa spatial ecology. First, individual variation in movement and space use is more a rule than an exception. Second, despite this variation, common patterns exist regarding seasonality of movement and right-skewed movement distributions. Third, rosy boa home ranges vary in size through time but remain in the same general location. Fourth, our data strongly suggest rosy boas do not show territoriality, and considerable overlap is common.

Individual Variation.—Despite consistent seasonal changes in movement, individual snakes exhibited high levels of variation in the daily timing of activity, proportional movement, and distances moved per day. For example, proportional movement at WAP varied from 0.29–0.77, whereas mean distance moved per day varied from 15.8–63.2 m. We do not know whether such differential spatial activity is common across snake species. For example, Shine (1987) also found individual variability in *Pseudochis porphyriacus*, whereas Plummer and Mills (2000) reported similar home range size and movement patterns among resident *Heterodon platirhinos*.

In our study, differences across individuals in the proportion of fixes collected during active and inactive seasons undoubtedly explain some of this variation. Shine (1987) suggested the large geographic extent of his study and a severe drought may have contributed to the observed variability across individuals. In our study, even animals coexisting within the same study site showed relatively large differences in space use and movement. Furthermore, we found no evidence body size affected space use. Thus, additional factors, such as reproductive activity, physiological state, or the density of rodents and rodent burrows within a home range, may have impacted space use.

Seasonality and Skewness in Movement.—Similar to Secor (1992), we found a decline in movement and activity during colder winter months. Surprisingly, the boas remained somewhat active during the fall, with rates of proportional movement similar to those in the spring and summer but with lower distances moved per day. Although rare, we observed boas above ground during November, December, and January. Other snake species in southern California may show less activity during cooler seasons than boas. For example, radio-tracked Red Diamond Rattlesnakes (*Crotalus ruber ruber*) studied concomi-

TABLE 4. Correlation coefficients between the distance moved (m) between fixes and the distance moved per day (m/day) when animals moved (movements of zero excluded). For each interval between a fix, we calculated both the distance moved and the distance moved per day. Sample size refers to the total number of intervals (total number of fixes = 1) used in each correlation.

Individual	Correlation coefficient	N	P
CNM-1	0.748	41	<0.001
MT-1	0.603	26	0.001
MT-2	0.478	4	0.522
MT-3	0.615	15	0.015
MT-4	0.591	9	0.093
MT-5	0.504	18	0.033
SM-1	0.832	44	0.001
WAP-1	0.684	96	0.001
WAP-2	0.562	30	0.001
WAP-3	0.171	12	0.595
WAP-4	0.571	37	0.001
WAP-7	0.647	55	0.001
WAP-9	0.840	40	0.001
WAP-10	0.756	50	0.001
WAP-11	0.451	42	0.03
WAP-12	0.808	33	0.001
WAP-15	0.860	27	0.001

tantly at WAP entered dens in mid-November and remained inactive typically until March (T. K. Brown, unpubl. data). Similarly, recent telemetry work on *Masticophis flagellum* showed animals below ground and inactive by September (M. J. Mitrovitch, unpubl. data). Also, Klauber (1939) found snake road kills began in March, peaked in May, and declined through September.

We observed right-skewed distributions in movement distances for all individuals; similar to those reported for *H. platirhinos* (Plummer and Mills, 2000). Right-skewed movement distributions are likely common in many species (see summarized case studies in Nathan et al., 2003), including small mammals (Diffendorfer et al., 1996), birds (Conner et al., 1997), butterflies (Baguette, 2003), plants (van der Pijl, 1982), and snakes (Plummer and Mills, 2000). Causes for right skewness include processes causing both the high frequency of short distance movements and processes causing rarer, longer movements.

For snakes, sleep and its associated inactivity, the ubiquity of some centrality in space use (i.e., home ranges or territories), and risk of predation all contribute to shorter distance movements. Movement patterns expressing a tendency to return toward a central location may be common in snakes because many recent studies, including ours, report such patterns (Shine, 1987; Webb and Shine, 1997; Reinert and Rupert, 1999; Johnson, 2000; Plummer and Mills, 2000; Whitaker and

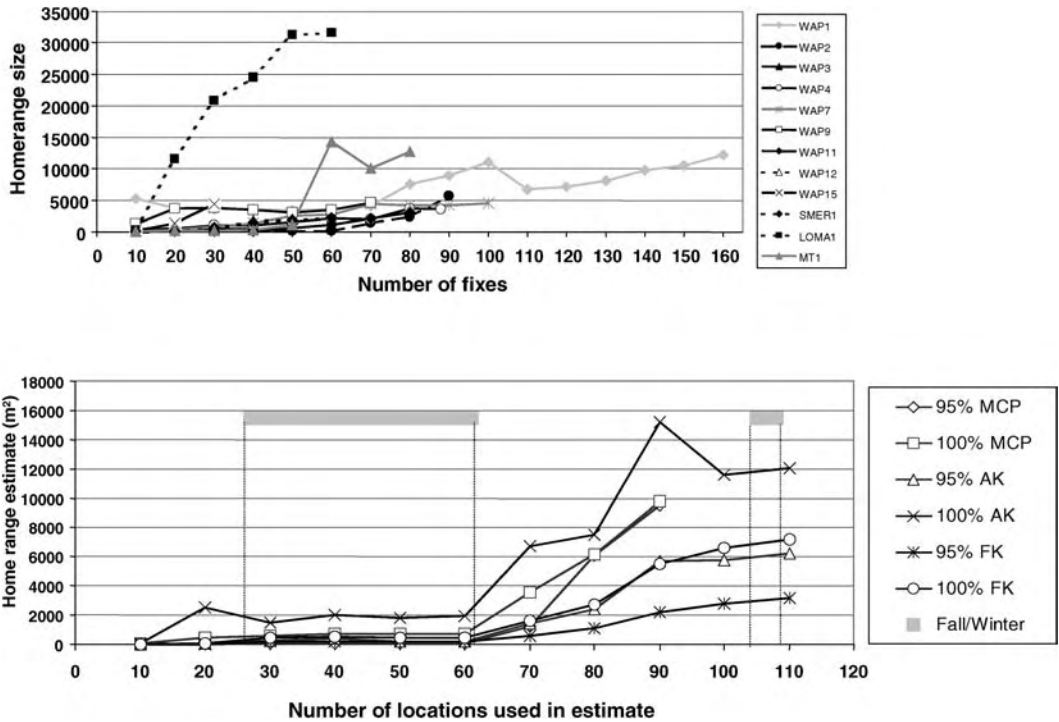


FIG. 2. Increase in home-range size estimated using the 95% adaptive kernel method with increased numbers of fixes. (A) represents all snakes across all time periods. (B) shows home-range size with increasing numbers of fixes for WAP 2. Home range was calculated using 95% or 100% of the data and either Minimum Convex Polygon (MCP), Adaptive Kernel (AK), or Fixed Kernel (FK) method. The gray bar at the top of the figure represents fall and winter. Other snakes showed similar patterns.

Shine, 2003). Although difficult to study, predation risk likely increases with time spent above ground and perhaps moving. For example, Reinert and Rupert (1999) showed declines in survivorship with longer distance movements for *Crotalus horridus*, and Bonnet et al. (1999) showed snake species with longer distance movements experienced greater mortality than sedentary species. As for rare, longer distance movements, factors have been reported for a number of snake species including searching for mates and migrating to seasonal hibernacula or gestation sites.

We spent considerable time on the issue of skewness because it should impact the statistics chosen and how one reports and analyzes movement data. Comparing movement patterns between species or between populations is surely a powerful tool for developing our understanding of snake movement ecology. However, building on Shine's (1987) recommendations, authors must report appropriate statistics given the properties of their movement data. Even recently, authors report estimates of distances moved per day using the two different methods

described in Table 3 (i.e., columns F vs. G in this paper, see Ashton 2003), which give different values when data are skewed.

We suggest future work report frequency distributions of movements (instead of simply their summary statistics) because the shapes of these distributions likely reflect a rich summation of trade-offs affected by both longer-term natural selection as well as more proximate environmental factors. Reporting only summary statistics may hide patterns evident in the shapes of these distributions. Contrasting how these distributions change through time, across degraded habitats, or across species and determining the processes causing their shape may lead to valuable insights.

Variability in Home-Range Size.—Regardless of the estimation method, we found home-range size increased with additional locations for all snakes and animals typically used substantial amounts of novel habitat each year. However, snakes tracked multiple years remained in the same general area, and only one snake had a home-range size greater than 1.5 ha, even after four years of data. Furthermore, within a period

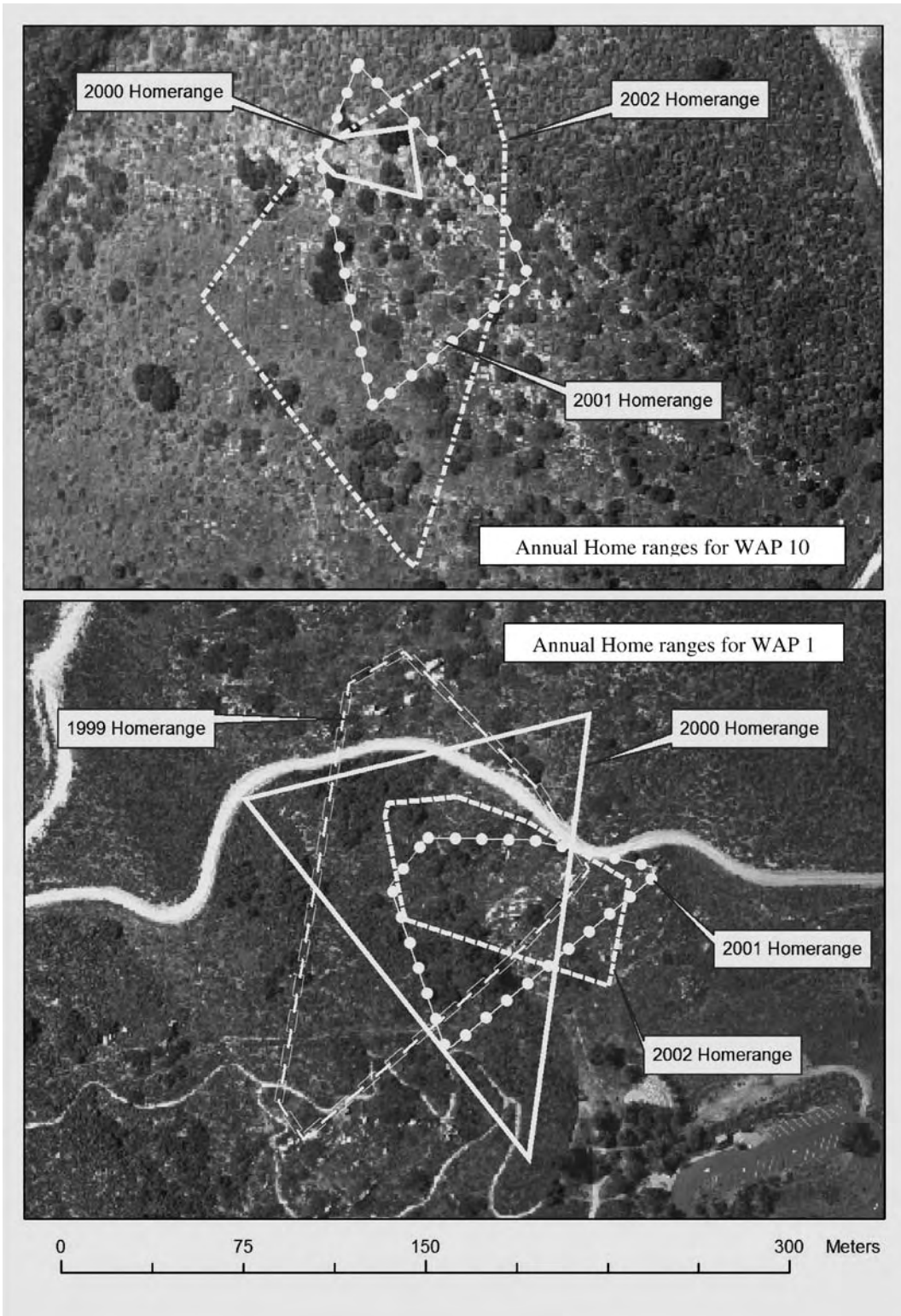


FIG. 3. Annual 100% minimum convex polygon home ranges for two male rosy boas at the Wild Animal Park. The home ranges show considerable overlap across years.

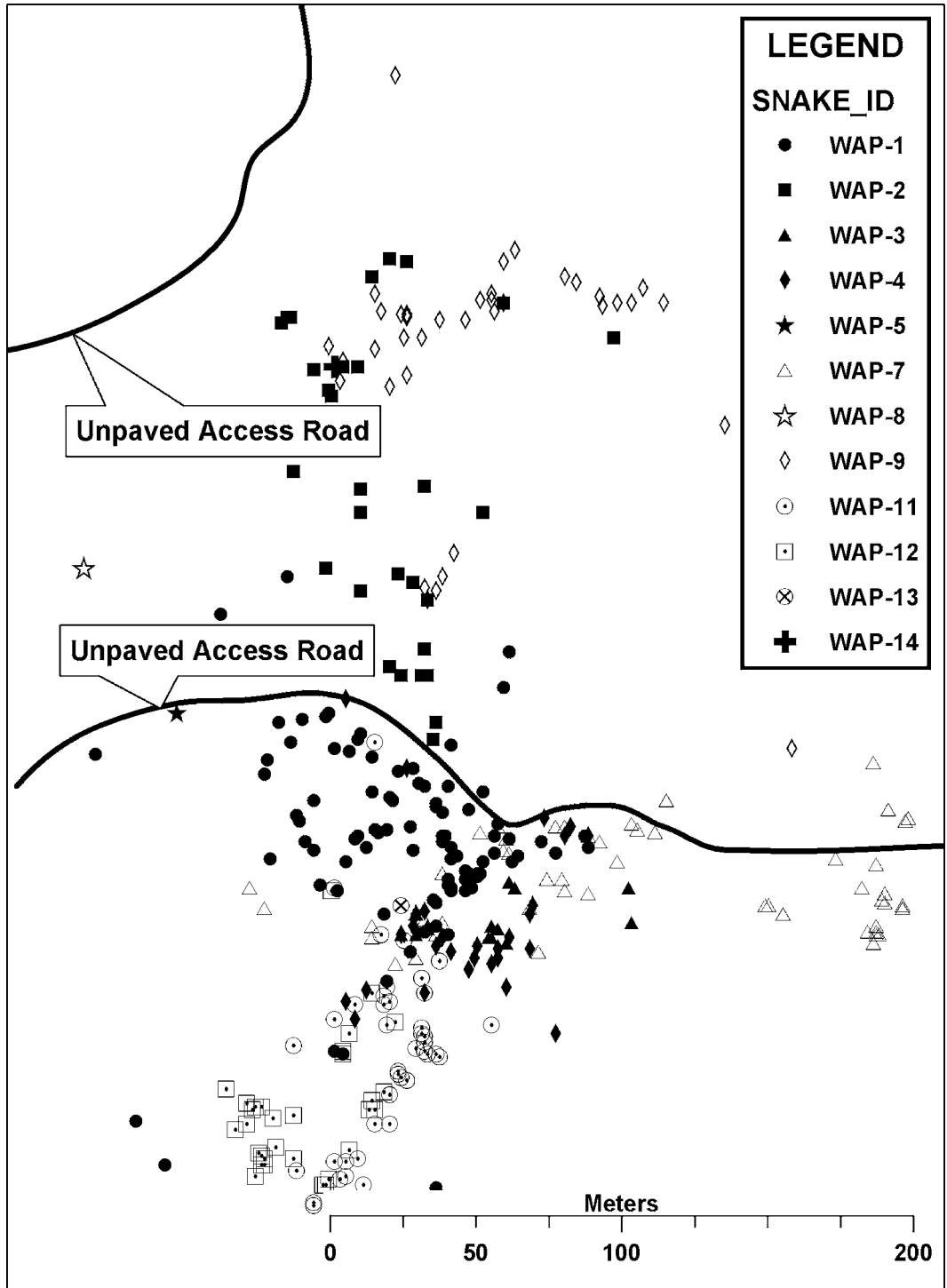


FIG. 4. Locations of 10 rosy boas tracked at the Wild Animal Park showing high levels of spatial overlap. Solid symbols are male snakes, and open symbols are female snakes.

of activity (spring and fall) snakes returned to particular sites and reused areas where they had already traveled. Thus, even with the rare long-distance movements, individuals had relatively fixed home ranges.

Notably, the home-range sizes for the boas in our study were smaller, relative to similarly sized snakes. Parizek et al.'s report (D. A. Parizek, P. C. Rose, C. R. Schwalbe, and C. H. Lowe, 1996, unpubl.) indicated an average Minimum Convex Polygon for six Mexican Rosy Boas (*Charina trivirgata trivirgata*) radio tracked for ~1 yr in Arizona of 1.8 ha \pm 0.52, very similar to our findings. We compared our home-range sizes to those reported by MacCartney et al. (1988) for similarly sized species with similar sampling efforts (species with larger home ranges but comparatively smaller sampling efforts were included but not vice versa). Of these 13 species, only three had smaller reported home ranges than the rosy boas (*Carphophis amoenus*, *Coronella austriaca*, and *Vipera aspis*). Within these 13 species, home ranges varied from 207.4 ha for *Crotalus horridus* to 0.18 ha for *V. aspis*, indicating factors beyond body size likely influence home-range size. Perhaps selective forces shaping the spatial ecology of different species and phylogenetic constraints explain the majority of this variation. Teasing apart the interplay between species plasticity and natural selection on movement patterns should lead to a greater understanding of the factors determining the large amounts of variation in snake movement patterns.

Lack of Territoriality and Habitat Use.—The observed spatial overlap among individuals and the multiple instances of sharing particular sites strongly suggest rosy boas are not territorial. In their 1996 unpublished study, D. A. Parizek, P. C. Rose, C. R. Schwalbe, and C. H. Lowe, found overlap in six Mexican Rosy Boas in Arizona. M. E. Dorcas (pers. comm.) also found considerable overlap and sharing of particular locations for rubber boas (*Charnia bottae*) observing six gravid females basking on one rock within 0.5 m of each other. We repeatedly found boas together with no evidence of conspecific avoidance as was seen for Stephens' banded snakes (*Hoplocephalus stephensis*; Fitzgerald et al., 2002).

Unlike the avoidance seen between male *Pituophis catenifer* (Rodriguez-Robles, 2003) or the spring time avoidance observed in male *Hoplocephalus bungaroides* (Webb and Shine, 1997), we found male rosy boas together with no sign of combat or displacement behavior throughout the entire study.

Acknowledgments.—The U.S. Geological Service Species at Risk Program, Cabrillo National Monument Foundation, and the San Diego State University Faculty Development Program

funded parts of this project. This project was identified as a high priority research need by the U.S. Fish and Wildlife Service, Office of Scientific Authority. We thank N. Scott and J. Tracey for help training C. Rochester with surgical procedures, and C. Brehme, J. Lemm, J.P. Montagne, S. Steward, D. Stokes, and others with collection of field data. T. Brown thanks A. Alberts for supporting the project. The Zoological Society of San Diego, National Park Service, San Diego State Field Stations, and Mission Trails Regional Park all allowed us access to land for the study, and we appreciate their help as well as staff support during the project. Two anonymous reviews improved the manuscript greatly. Finally, we thank D. Grey for developing SnakeByte software and capturing a rosy boa only 24 hours after setting foot in the United States.

LITERATURE CITED

- ALEKSIUK, M. 1977. Cold-induced aggregative behavior in the Red-Sided Garter Snake (*Thamnophis sirtalis parietalis*). *Herpetologia* 33:98–101.
- ALEKSIUK, M., AND P. T. GREGORY. 1974. Regulation of seasonal mating behavior in *Thamnophis sirtalis parietalis*. *Copeia* 1974:681–689.
- ASHTON, K. G. 2003. Movements and mating behavior of adult male Midget Faced Rattlesnakes, *Crotalus oreganus concolor*, in Wyoming. *Copeia* 1:190–194.
- BAGUETTE, M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography* 26:153–160.
- BLUNDELL, G. M., J. A. K. MAIER, AND E. M. DEBEVEC. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* 71:469–489.
- BONNET, X., G. NAULLEAU, AND R. SHINE. 1999. The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* 89:39–50.
- BROWN, G. P., AND P. J. WEATHERHEAD. 2000. Thermal ecology and sexual size dimorphism in Northern Water Snakes, *Nerodia sipedon*. *Ecological Monographs* 70:311–330.
- CASE, T. J., AND R. N. FISHER. 2001. Measuring and predicting species presence: coastal sage scrub case study. In C. T. Hunsaker, M. F. Goodchild, M. A. Friedl, and T. J. Case (eds.), *Spatial Uncertainty in Ecology*, pp. 47–71. Springer-Verlag, New York.
- CONNER, R. N., D. C. RUDOLPH, R. R. SCHAEFER, AND D. SAENZ. 1997. Long-distance dispersal of Red-Cockaded Woodpeckers in Texas. *Wilson Bulletin* 109:157–160.
- DANIELSON, B. J. 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. *American Naturalist* 138:1105–1120.
- . 1992. Habitat selection, interspecific interactions, and landscape composition. *Evolutionary Ecology* 6:399–411.
- DIFFENDORFER, J. E. 1998. Testing models of source-sink dynamics and balanced dispersal. *Oikos* 81:417–433.
- DIFFENDORFER, J. E., R. D. HOLT, N. A. SLADE, AND M. S. GAINES. 1996. Small mammal community patterns in old fields; distinguishing site-specific from re-

- gional processes. In M. L. Cody and J. A. Smallwood (eds.), *Long-Term Studies of Vertebrate Communities*, pp. 421–466. Academic Press, San Diego, CA.
- DONCASTER, C. P., J. CLOBERT, B. DOLIGEZ, L. GUSTAFSSON, AND E. DANCHIN. 1997. Balanced dispersal between spatially varying local populations: an alternative to the source-sink model. *American Naturalist* 150:425–445.
- DORCAS, M. E. 1995. Testing the Coadaptation Hypothesis: The Thermoregulatory Behavior and Thermal Physiology of the Rubber Boa (*Charina bottae*). Unpubl. Ph.D. diss., Idaho State Univ., Pocatello.
- DORCAS, M. E., AND C. R. PETERSON. 1998. Daily body temperature variation in free-ranging Rubber Boas. *Herpetologica* 54:88–103.
- DORCAS, M. E., C. R. PETERSON, AND M. E. T. FLINT. 1997. The thermal biology of digestion in Rubber Boas (*Charina bottae*): physiology, behavior, and environmental constraints. *Physiological Zoology* 70: 292–300.
- DUVALL, D., M. B. KING, AND M. J. GUTZWILLER. 1985. Behavioral ecology and ethology of the Prairie Rattlesnake. *National Geographic Research* 1: 80–111.
- FAHRIG, L., AND J. E. PALOHEIMO. 1987. Interpatch dispersal of the cabbage butterfly. *Canadian Journal of Zoology* 65:616–622.
- FISHER, R. N., AND T. J. CASE. 2000. Distribution of the herpetofauna of coastal southern California with reference to elevation effects. In J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham (eds.), *Second Interface between Ecology and Land Development in California*, pp. 137–143. U.S. Geological Survey Open-Fire Report 00-62, Sacramento, CA.
- FITZGERALD, M., R. SHINE, AND F. LEMCKERT. 2002. Spatial ecology of arboreal snakes (*Hoplocephalus stephensii*, Elapidae) in an eastern Australian forest. *Austral Ecology* 27:537–545.
- GREGORY, P. T. 1984. Communal denning in snakes. In R. A. Seigel, L. E. Hunt, J. L. Knight, L. Malaret, and N. L. Zuschlag (eds.), *Vertebrate Ecology and Systematics: A Tribute to Henry S. Fitch*, pp. 57–75. Museum of Natural History Special Publications, Univ. of Kansas, Lawrence.
- GREGORY, P. T., J. M. MACCARTNEY, AND K. W. LARSEN. 1987. Spatial patterns and movements. In R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 366–395. Macmillan, New York.
- HANSKI, I., T. PAKKALA, M. KUUSAAARI, AND G. LEI. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* 72: 21–28.
- HARDY, D. L., AND H. W. GREENE. 1999. Surgery on rattlesnakes in the field for implantation of transmitters. *Sonoran Herpetologist* 12:26–28.
- HOLT, R. D. 2003. On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* 5:159–178.
- HOOGE, P. N., AND B. EICHENLAUB. 1997. Animal movement extension to ArcView. Vers. 2.0. Alaska Science Center-Biological Science Office, U.S. Geological Survey, Anchorage.
- HUEY, R. B., C. R. PETERSON, S. J. ARNOLD, AND W. P. PORTER. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70:931–944.
- HUFFAKER, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343–383.
- HUNTER, R. D., R. N. FISHER, AND K. R. CROOKS. 2003. Landscape-level connectivity in coastal southern California, USA as assessed through carnivore habitat suitability. *Natural Areas Journal* 23:302–314.
- JENKINS, L. N., T. J. THOMASSON, AND J. G. BYRD. 2001. A field study of the Black Kingsnake, *Lampropeltis getula nigra*. *Herpetological Natural History* 8:57–67.
- JOHNSON, G. 2000. Spatial ecology of the Eastern Massauga (*Sistrurus c. catenatus*) in a New York peatland. *Journal of Herpetology* 34:186–192.
- KEDDY, P. A. 1981. Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *Journal of Ecology* 69:615–630.
- . 1982. Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. *Oecologia* 52:348–355.
- KLAUBER, L. M. 1939. Studies of reptile life in the arid Southwest. *Bulletins of the Zoological Society of San Diego* 14:100.
- MACCARTNEY, J. M., P. T. GREGORY, AND K. W. LARSEN. 1988. A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology* 22:61–73.
- NATHAN, R., G. PERRY, J. T. CRONIN, A. E. STRAND, AND M. L. CAIN. 2003. Methods for estimating long-distance dispersal. *Oikos* 103:261–273.
- PLUMMER, M. V., AND N. E. MILLS. 2000. Spatial ecology and survivorship of resident and translocated Hognose Snakes (*Heterodon platirhinos*). *Journal of Herpetology* 34:565–575.
- PRINGLE, R. M., J. K. WEBB, AND R. SHINE. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84:2668–2679.
- PULLIAM, R. H. 1988. Source, sinks and population regulations. *American Naturalist* 132:652–661.
- PUSEY, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution* 2:295–299.
- REINERT, H. K. 1993. Habitat selection in snakes. In R. A. Seigel (ed.), *Snakes: Ecology and Behavior*, pp. 201–240. McGraw-Hill, Inc, New York.
- REINERT, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 3:702–705.
- REINERT, H. K., AND R. R. J. RUPERT. 1999. Impacts of translocation on behavior and survival of Timber Rattlesnakes, *Crotalus horridus*. *Journal of Herpetology* 33:45–61.
- RODRIGUEZ-ROBLES, J. A. 2003. Home ranges of gopher snakes (*Pituophis catenifer*, Colubridae) in central California. *Copeia* 2003:391–396.
- RODRIGUEZ-ROBLES, J. A., C. J. BELL, AND H. W. GREENE. 1999. Gape size and evolution of diet in snakes: feeding ecology of erycine boas. *Journal of the Zoological Society of London* 248:49–58.
- SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for homerange analysis. *Ecology* 77:2075–2085.

- SECOR, S. M. 1992. Activities and Energetics of a Sit-and-Wait Foraging Snake, *Crotalus cerastes*. Unpubl. Ph.D. diss. Univ. of California, Los Angeles.
- SHINE, R. 1987. Intraspecific variation in thermoregulation, movements and habitat use by Australian Blacksnakes, *Pseudechis porphyriacus* (Elapidae). *Journal of Herpetology* 21:165–177.
- STEBBINS, R. C. 2003. *Western Reptiles and Amphibians*. 3rd ed. Houghton Mifflin, Boston, MA.
- TRENHAM, P. C., W. D. KOENIG, AND H. B. SHAFFER. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. *Ecology* 82:3519–3530.
- VAN DER PIJL, L. 1982. *Principles of Dispersal in Higher Plants*. Springer-Verlag, Berlin, Germany.
- WATKINSON, A. R., W. M. LONSDALE, AND M. H. ANDREW. 1989. Modelling the population dynamics of an annual plant *Sorghum intrans* in the wet-dry tropics. *Journal of Ecology* 77:162–181.
- WEBB, J. K., AND R. SHINE. 1997. A field study of spatial ecology and movements of a threatened snake species, *Hoplocephalus bungaroides*. *Biological Conservation* 82:203–217.
- WHITAKER, P. B., AND R. SHINE. 2002. Thermal biology and activity patterns of the Eastern Brownsnake (*Pseudonaja textilis*): a radiotelemetric study. *Herpetologica* 58:436–452.
- . 2003. A radiotelemetric study of movements and shelter-site selection by free ranging brown-snakes (*Pseudonaja textilis*, Elapidae). *Herpetological Monographs* 17:130–144.
- WYNNE-EDWARDS, V. C. 1967. *Animal Dispersion in Relation to Social Behaviour*. Hafner Publishing Co., New York.

Accepted: 3 October 2004.

Journal of Herpetology, Vol. 39, No. 1, pp. 36–42, 2005
Copyright 2005 Society for the Study of Amphibians and Reptiles

Ecology and Reproduction of *Anolis capito* in Rain Forest of Southeastern Nicaragua

LAURIE J. VITT¹ AND PETER A. ZANI²

*Sam Noble Oklahoma Museum of Natural History and Department of Zoology,
University of Oklahoma, Norman, Oklahoma 73072-7029, USA*

ABSTRACT.—We studied the ecology of *Anolis capito* in the rain forest of southeastern Nicaragua during late dry season of 1993. These cryptic anoles live low on trunks in shaded rain forest and are active throughout the day but appear to spend most of their time in shade. Body temperatures averaged $28.8 \pm 0.5^\circ\text{C}$, which is 1.3°C higher than substrate temperatures and 1.7°C higher than air temperatures. Females were larger and reach sexual maturity at a larger SVL than males. Females in late dry season often contain two oviductal eggs that differed in shell condition indicating that they were not ovulated simultaneously. Females had evidence of as many as four clutches (two oviductal eggs and two different-sized enlarged vitellogenic follicles) suggesting rapid clutch production. The diet consists of a variety of invertebrates, with grasshoppers, homopterans, insect larvae, and roaches dominating volumetrically. On average, these lizards contained 1.6 ± 0.1 prey items. Prey size varied with lizard size, but no sexual differences existed. These lizards appear to capture a small number of large prey. Many ecological and life-history traits of *A. capito* are similar to those of other *Anolis* lizards suggesting an historical origin.

As more and more tropical forest regions experience deforestation or other habitat modification, ecological studies of individual species, species assemblages, communities, and entire

ecosystems increase in importance. Establishing the “value” of tropical ecosystems requires data on resident species such that decisions on forest “development” can be made with the best possible ecological information. Descriptive ecological studies of lizards are important because “(1) basic ecological data are lacking for most species; (2) ecological data provide the basis for understanding the role of each species in

¹ Corresponding Author. E-mail: vitt@ou.edu

² Present address: Department of Integrative Physiology, 354 University of Colorado, Boulder, Colorado 80309-0354, USA.

complex ecosystems; (3) ecological data can be used in phylogenetic analyses that synthesize data from many studies and trace the evolutionary history of such traits; and (4) ecological data provide an arsenal for defending the value of natural ecosystems when drastic habitat alteration is considered" (Vitt et al., 2003a).

Central American moist forests are among the Earth's most endangered ecoregions (Mittermeier et al., 2000) and have experienced rapid conversion to agriculture following deforestation even though detailed studies on many resident species are lacking. The natural history of many Central American rain forest species has been summarized by various authors (Rand and Myers, 1990; see chapters in Janzen, 1983), and a number of detailed ecological studies have provided insight into the value of individual species for understanding biological processes (e.g., Andrews and Rand, 1984; Andrews et al., 1983; Guyer, 1988a,b). The vast majority of studies on Caribbean rain forest lizards have taken place in Costa Rica or Panama, most likely a result of ease of access, availability of well-equipped field stations, and a high level of funding that has been directed toward studies in these two areas. Studies in other regions should be of particular interest because they provide a yardstick against which to examine geographic variation in ecological traits.

In an earlier paper, we compared ecology of all lizard species occurring just north of the Río San Juan in Nicaragua (Vitt and Zani, 1998). The primary intent of that paper was to provide a community-level analysis of rainforest lizard diets, with very little detail on individual species. In this paper, we describe the ecology of one species, *Anolis capito* in much more detail. Although *A. capito* (as *Norops capito*) was listed as a species occurring in rain forest of Costa Rica by Scott et al. (1983) and indicated as a potential predator on another anole (*Anolis polylepsis*) by Andrews (1983), no ecological information was included. Savage (2002) described *A. capito* as an anole inhabiting "relatively undisturbed Lowland Moist and Wet Forests and Premontane Wet Forest and Rainforest." It is arboreal, perching low on tree trunks, a thermoconformer, and reproduces year round (see also Fitch 1975; Corn, 1981; Fitch and Seigel, 1984). *Anolis capito* is a species for which little detailed ecological data have been published.

MATERIALS AND METHODS

Study Site, Sampling, Microhabitats, Activity, and Thermal Ecology.—We conducted this study in Caribbean rainforest near the north bank of the Río San Juan in Río San Juan Province, Nicaragua, between 13 March and 20 April of 1993 (Vitt and Zani, 1998), which is late in the dry

season. Most of the study site was undisturbed, but a few small patches of slightly disturbed forest were included in our sampling. For each lizard, we recorded habitat (primary or secondary forest), microhabitat (tree trunks or leaf litter; although other microhabitats were available, none was used by *A. capito*), and height off ground and perch (trunk) diameter in centimeters. We also recorded whether lizards were in sun, shade, or active under clouds. We collected all lizards by hand. Within 30 sec of capture, we took lizard body temperature (T_b) with a Miller-Weber rapid-register thermometer. We also recorded air (T_a) and substrate (T_{ss}) temperatures at the point of capture. Upon return to our field laboratory, we euthanized lizards with a lethal injection of Nembutal.

Morphology and Reproduction.—We took the following relevant measurements on all lizards prior to fixation: snout-vent length (SVL), tail length, and length of regenerated tail portion (if any) to 1.0 mm with a metric rule; total mass (0.1 g) with Pesola spring balances; head width, length, and height, body width and height, and hindleg length (0.1 mm) with dial calipers. We individually tagged all lizards and preserved them in 10% formalin. Within two weeks of capture, lizards were dissected and sex was determined on the basis of reproductive organs. Males were considered sexually mature if they contained enlarged testes and distended epididymides. Females were considered sexually mature if they contained vitellogenic follicles and/or oviductal eggs. We counted the number of oviductal eggs, assigned them to left or right oviduct, and measured (length and width to 0.01 mm), towel dried, and weighed them to 0.1g. We noted whether shell was present or absent. We calculated oviductal egg volume as:

$$V = \pi LW^2(3c^2 + 14c + 35)/210,$$

where L is egg length, W is egg width, and $c = \lambda(\sqrt{E} - 1)$. We estimated E for individual eggs by dividing egg length by width and λ was estimated as 0.25 by comparing the shape of *A. capito* eggs with models in Maritz and Douglas (1994). We also counted and measured vitellogenic follicles and noted whether they were in the left or right ovary. We estimated relative clutch mass as oviductal egg mass/body mass (Vitt and Congdon, 1978). Finally, we estimated the minimum number of clutches a female could produce by totaling up the number of oviductal eggs and enlarged vitellogenic follicles.

We performed a Mann-Whitney U -test on SVL and mass of adults to test for sexual dimorphism in size. To test for sexual differences in other morphological traits, we \log_{10} -transformed all morphological variables. We then performed analyses of covariance (ANCOVA) on each

morphological variable with SVL as the covariate and sex as the class variable.

Diet.—We removed stomachs from lizards, separated prey items on a Petri dish, identified them to family level when possible (all were identified at least to order), and measured length and width of each prey item to 0.1 mm with dial calipers. Prey categories for analysis were: Colembola, Orthoptera, Blattaria, Phasmatida, Homoptera, Coleoptera, Lepidoptera, Diptera, ants, insect larvae, spiders, Diplopoda, Chilopoda, Isopoda, and lizards. We estimated volumes of individual prey with the formula for a prolate spheroid:

$$V = 4/3\pi(L/2)(W/2)^2,$$

where L = prey length and W = prey width. We consider this a reasonable procedure because prey in the stomach are tightly packed, with limbs and wings pressed against the body, thus presenting the minimum possible volume. We used the computer program BugRun, a 4th dimension-based analysis, to produce the dietary summary, calculate mean prey size (length, width, and volume) for each lizard, estimate stomach volume based on total prey volume, and calculate niche breadth using the inverse of Simpson's (1949) measure (Pianka, 1975):

$$\beta = 1 / \sum_{i=1}^n p_i^2,$$

where p is the proportional utilization of each prey type i . Niche breadth values (β) vary from 1 (exclusive use of a single prey type) to n (even use of all prey). Output from BugRun includes a summary of mean prey length, width, and volume for each individual lizard.

We examined the effect of lizard size on prey size and number of prey eaten by first \log_{10} -transforming mean prey volume, number of prey per stomach, and lizard size data and then performing a regression analysis on the \log_{10} transformed variables with \log_{10} -SVL as the independent variable. We compared prey size and number of prey eaten between sexes with an ANCOVA with lizard \log_{10} -SVL as the covariate and sex as the class variable.

All lizards were ultimately transferred to 70% ethanol for permanent storage and deposited in the Sam Noble Oklahoma Museum of Natural History (OMNH) or the National Museum of Nicaragua in Managua. Means are presented throughout ± 1 SE.

RESULTS AND DISCUSSION

Habitat Use and Thermal Ecology.—In lowland rainforest of southeastern Nicaragua, *A. capito* occurs in undisturbed and slightly disturbed rain forest, where it resides low on trunks of relatively

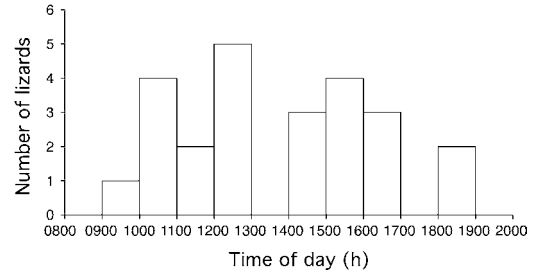


FIG. 1. Daily activity cycle of *Anolis capito* in southeastern Nicaragua based on field observations of active lizards.

small trees. Among 26 individuals for which we collected habitat and microhabitat data, 24 (92.3%) were in primary forest, and two (7.7%) were in secondary forest. Individuals are most frequently observed off the ground, but they occasionally descend to the ground, most likely to capture insects (see Savage, 2002). Nineteen (73.1%) of those were first observed on tree trunks, and seven (26.9%) were on leaf litter. The 19 on tree trunks averaged 45.8 ± 7.2 (12–120) cm off the ground. Diameter of trunks on which lizards were found averaged 7.9 ± 3.0 (1–60) cm. Four of 22 (18.2%) lizards were in sun when first observed, 16 (72.7%) were in shade, and two (9.1%) were active under clouds. Lizards were found on tree trunks or in leaf litter through most of the day (Fig. 1). They are cryptic in morphology and color, resembling a patch of lichens on the tree trunk.

Body temperatures (T_b) of 16 lizards averaged $28.9 \pm 0.4^\circ\text{C}$ with corresponding T_{ss} and T_a averaging $27.7 \pm 0.4^\circ\text{C}$ and $27.4 \pm 0.5^\circ\text{C}$, respectively. Although a significant relationship existed between lizard T_b and both T_{ss} ($R^2 = 0.662$, $F_{1,15} = 19.8$, $P = 0.0001$) and T_a ($R^2 = 0.425$, $F_{1,15} = 12.1$, $P = 0.0037$), lizard T_b averaged $1.3 \pm 0.3^\circ\text{C}$ higher than T_{ss} and $1.5 \pm 0.3^\circ\text{C}$ above T_a . The relationship between T_b and T_{ss} is $T_b = 11.011 + 0.647 (T_{ss})$. Even though lizard T_b was tightly correlated with T_{ss} and T_a , lizard T_b averages slightly higher than T_{ss} or T_a suggesting that some basking takes place for heat gain. This is also suggested by observations that 18% of lizards were first encountered in sun. T_b is low relative to many Neotropical lizard species that occupy forest clearings or treefalls (e.g., *Ameiva festiva*, Vitt and Zani, 1996a; *Kentropyx calcarata* and *Mabuya nigropunctata*, Vitt et al., 1997a), but similar to lizards that occupy shaded microhabitats within undisturbed rain forest (e.g., *Anolis nitens* [as *Anolis chrysolepis*], Vitt and Zani, 1996b; Vitt et al., 2001; *Anolis trachyderma*, Vitt et al., 2002; *Gonatodes hasemani* and *Gonatodes humeralis*, Vitt et al., 1997b, 2000; *Neusticurus juruazensis* and *Neusticurus ecleopus*; Vitt and

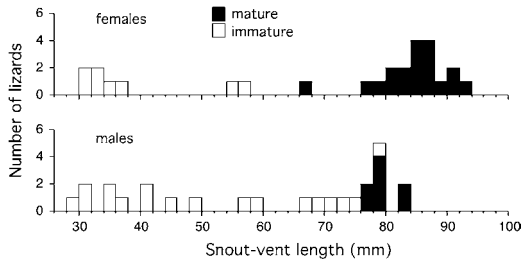


FIG. 2. Distribution of SVL for *Anolis capito* in southeastern Nicaragua.

Avila-Pires, 1998; Vitt et al., 1998). Thus, for the most part, our quantitative data are consistent with Savage's (2002) qualitative description of habitat use and thermal ecology of *A. capito*.

Morphology.—Thirty captured females averaged 70.3 ± 4.3 mm SVL (Fig. 2) and weighed 9.2 ± 1.1 g. The largest female measured 92 mm SVL (Fig. 2) and weighed 15.5 g. Twenty-nine males captured averaged 59.5 mm SVL and weighed 5.6 ± 0.8 g. The largest male measured 82 mm SVL and weighed 11.2 g. Among adult lizards, females had larger SVL (Mann-Whitney U , $Z = -4.2$, $P < 0.0001$) and mass (Mann-Whitney U , $Z = -4.4$, $P < 0.0001$) than males. Adult females averaged 84.8 ± 0.9 mm SVL and weighed 12.8 ± 0.4 g. Adult males averaged 77.1 ± 1.0 mm SVL and weighed 9.4 ± 0.5 g. No sexual differences were detected in mass (ANCOVA, $F_{1,49} = 2.7$, $P = 0.1066$), head width (ANCOVA, $F_{1,49} = 2.5$, $P = 0.1202$), or head length (ANCOVA, $F_{1,49} = 2.5$, $P = 0.1170$) independent of those associated with differences in SVL. However, males had longer forelegs and hind legs than females independent of SVL (ANCOVA, all P -values < 0.001). Thus the only apparent sexual dimorphism appears to be in adult body size (SVL and mass) and relative limb lengths. Similar sexual differences have been observed in some other lizard species (e.g., three subspecies of *Anolis nitens*; Vitt et al., 2001). The function of relatively longer limbs in male lizards remains unknown, but may be associated with bobbing, dewlap extension, and other social behaviors of males that involve lifting the front part of the body. Consequently, it may be attributable to sexual selection if males with relatively longer forelimbs have greater reproductive success as a result. This remains to be determined. Male *A. capito* reach sexual maturity at a smaller size than females, which might account for their smaller size through life. When males are the larger sex, sexual dimorphism usually is attributed to sexual selection (e.g., Jenssen, 1970; Stamps, 1983; Vitt et al., 1995). In *Anolis* species with females larger than males (e.g., Vitt et al., 2001, 2002, 2003a), large female

size may allow females to produce larger eggs (see Andrews and Rand, 1974) and it could allow more rapid clutch production. Apparently, in *A. capito*, as in some other anoles (e.g., *A. nebulosus*; Ramírez-Bautista and Vitt, 1997), the advantages to large male size (increased ability to secure mates; Ruby, 1981) outweigh the advantages to large female size (e.g., ability to produce larger eggs or produce eggs at a more rapid rate; Andrews and Rand, 1974).

Reproduction.—Seventeen females contained one of several possible combinations of oviductal eggs and enlarged vitellogenic follicles. Eight contained two oviductal eggs, one with shell and one without, and one contained two shelled oviductal eggs. In the latter, one egg had a more developed shell than the other. Among the 17 reproductive females, nine contained a combination of oviductal eggs and vitellogenic follicles suggesting a minimum of three clutches and eight showed similar evidence of four clutches (two oviductal eggs and two enlarged vitellogenic follicles). Overall mean number of minimum potential clutches was 3.5 ± 0.13 . Presence of two oviductal eggs and, in many instances, two additional vitellogenic follicles (four sequential clutches) in female *A. capito* suggests that clutches may be produced in rapid succession. Although we do not know the amount of time between clutches in *A. capito*, some anoles are known to produce an egg every seven days (Andrews, 1985). Rapid clutch production may reflect seasonally high abundance of resources (Ballinger, 1977). Alternately, some combination of day length, temperature, and moisture may signal that the dry season is coming to an end, and as a result, females begin producing clutches in rapid succession. If so, then high resources associated with the wet season may be most important for hatchlings. Andrews and Sexton (1981) found that warm temperatures, which signaled drought conditions, caused *A. limifrons* and *A. auratus* to curtail reproduction. Thus reproductive response to immediate environmental conditions appears likely in *A. capito* as well.

The difference in size of shelled versus unshelled oviductal eggs was reflected mostly in egg length (Table 1) which translated into large differences in egg volume and mass; freshly ovulated eggs did not differ in width from shelled eggs ready to be deposited. Among females with two oviductal eggs, only one was in each oviduct. Both the difference in presence of shell and size indicates that each oviductal egg was ovulated at a different time (allochronic pattern of Smith et al., 1973). Mass of shelled oviductal eggs was not correlated with lizard SVL ($r_s = 0.078$, $P = 0.837$) or lizard mass ($r_s = 0.231$, $P = 0.540$).

Reproduction in *A. capito* appears similar to most anoles studied. Eggs ovulated allochroni-

TABLE 1. Body size and reproductive characteristics of female *Anolis capito* containing two oviductal eggs. In all cases but one, one oviductal egg (first clutch) had a shell; the other did not (second clutch). For the individual containing two eggs with shells in different stages, we considered the more developed shelled egg as the first clutch. These females averaged 85.3 ± 1.6 mm SVL and weighed 13.5 ± 1.5 g in total mass. Oviductal eggs elongate but do not change width as they mature. First eggs averaged 0.16 ± 0.032 g heavier than second eggs.

Characteristic	First clutch	Second clutch	F-value	P-value
Egg mass (g)	0.60 ± 0.03	0.44 ± 0.30	18.8	0.0007
Egg length (mm)	17.46 ± 0.49	15.45 ± 0.35	11.6	0.0053
Egg width (mm)	7.95 ± 0.16	7.28 ± 0.34	2.5	0.1392
Egg volume (mm ³)	606.07 ± 24.30	453.47 ± 39.62	10.8	0.0054
	1 egg	2 eggs	F-value	P-value
Relative clutch mass	0.045 ± 0.003	0.077 ± 0.004	46.9	< 0.0001

cally (Smith et al., 1973) in rapid succession (e.g., Gordon, 1956; Tinkle, 1969; Andrews, 1985), based on the observation that two eggs with different shell conditions were often present (one in each oviduct) and two vitellogenic follicles (one in each ovary) were also present. Thus, clutch size based on number of eggs produced during an oviposition event is one egg (Fitch, 1970, 1982; Tinkle et al., 1970). This points to the importance of closely examining condition of oviductal eggs in lizards to be certain that the number of eggs estimated for a clutch in dissected females accurately reflects the number of eggs that will be deposited in a single oviposition event. In anoles, clutch size is a single egg even though more than one egg may be represented in oviducts. Like other anoles (Tinkle et al., 1970; Vitt and Congdon, 1978; Vitt and Price, 1982), RCM is low if the single shelled egg is used for the calculation. If both oviductal eggs are used, RCM is still relatively low compared to lizards that produce clutches of several or many eggs.

Diet.—A variety of insects and other invertebrates were eaten by *A. capito*. Forty-three lizards contained 67 individual prey comprising 15 different prey types. Prey averaged 15.42 ± 0.98 (2.84–39.64) mm in length, 4.00 ± 0.25 (0.67–10.78) mm in width, and 199.75 ± 35.15 (0.88–1813.23) mm³ in volume. In general, these lizards ate few, relatively large prey items. Prey size varies considerably among *Anolis* lizards, with some Central American species, such as *A. limifrons* and *A. humilis* and South American species such as *A. fuscauratus* eating many small prey and others, such as *A. biporcatus* and *A. capito* eating a few relatively large prey (Vitt and Zani, 1998). *Anolis* lizards that eat large prey often eat small lizards as well (e.g., Savage 2002; Vitt et al., 2003a,b). On average, lizards contained 1.6 ± 0.1 (range 1–4) prey items. The diet of *A. capito* was dominated numerically by insect larvae and grasshoppers (Table 2). Volumetrically, grasshoppers, homopterans, insect larvae, and roaches dominated. Insect larvae and grasshoppers were eaten by most of the lizards

TABLE 2. Summary of the diet of *Anolis capito* from southeastern Nicaragua.

Prey type	N	% N	Volume	% Vol.	Frequency
Collembola	4	5.97	14.52	0.11	2
Orthoptera	12	17.91	3356.51	25.08	12
Blattaria	5	7.46	1580.91	11.81	5
Phasmatida	2	2.99	433.31	3.24	2
Homoptera	3	4.48	3296.64	24.63	2
Coleoptera	5	7.46	714.34	5.34	5
Lepidoptera	2	2.99	134.3	1.00	2
Diptera	3	4.48	321.8	2.40	3
Ants	3	4.48	16.57	0.12	3
Insect larvae	17	25.37	1604.49	11.99	15
Spiders	3	4.48	969.88	7.25	3
Diplopoda	5	7.46	375.72	2.81	5
Chilopoda	1	1.49	163.89	1.22	1
Isopoda	1	1.49	96.65	0.72	1
Lizards	1	1.49	303.62	2.27	1
SUMS	67	100	13383.15	100	—
Niche breadths		7.86		6.13	

sampled. Mean prey volume per lizard was correlated with lizard SVL ($F_{1,39} = 91.4$, $P < 0.0001$), but no sexual differences in mean prey volume independent of SVL were found (ANCOVA, with SVL as covariate and sex as the class variable, $F_{1,39} = 0.08$, $P = 0.7854$). Likewise, no sexual difference in number of prey independent of SVL was apparent (ANCOVA, with SVL as covariate and sex as the class variable, $F_{1,39} = 1.32$, $P = 0.2581$). A significant relationship existed between stomach contents volume and lizard SVL ($R^2 = 0.71$, $F_{1,41} = 105.3$, $P < 0.0001$), but little variation exists in stomach contents volume independent of SVL. Thus smaller lizards were equally as full as larger lizards. The equation describing the relationship between lizard size and full stomach volume is: \log_{10} stomach volume = $3.627 (\log_{10}\text{-SVL}) - 4.368$. This, coupled with the observation that all captured lizards had prey in their stomachs, suggests that they typically were in positive energy balance (Huey et al., 2001).

CONCLUSIONS

Many ecological and life-history traits of *A. capito* are similar to those of certain other *Anolis* lizards. These include arboreality restricted to tree trunks, shade dwelling, relatively low active body temperatures, and lichen-like cryptic morphology. Still other characteristics are similar to those of all anoles, including allochronic ovulation of eggs and oviposition of a single egg at a time. These similarities likely reflect characteristics of ancestors of *A. capito* at varying levels within the evolutionary history of anoles (e.g., Vitt et al., 2003c). A phylogenetic analysis of ecological traits of anoles may identify the origins of ecological traits within anoles, shedding considerable light on their ecological history.

Habitat modification that reduces the canopy, exposing more of the forest floor to sun likely would have a detrimental effect on populations of *A. capito* because *A. capito* possess a set of ecological traits (shade seeking, low T_b , trunk dwelling) associated with presence of tropical rainforest. The observation that these lizards are not found in open habitat patches alone suggests their dependency on relatively undisturbed rainforest. This species will likely disappear with elimination of rainforest canopy.

Acknowledgments.—We first thank M. Camacho of the Departamento de Fauna Silvestre of Nicaragua for making this research possible, providing excellent logistic aid, and issuing collecting and export permits. R. D. Durtsche and J. P. Caldwell of the University of Oklahoma and R. Perez of the Departamento de Fauna Silvestre aided in the field. Financial aid for this and other Nicaraguan studies stemmed from

a research grant from the Faculty Research Council at the University of Oklahoma to LJV and J. P. Caldwell.

LITERATURE CITED

ANDREWS, R. M. 1983. *Norops polylepis* (Lagartija, Anole, *Anolis* Lizard). In D. H. Janzen (ed.), Costa Rican Natural History, pp. 409–410. Univ. of Chicago Press, Chicago.

———. 1985. Oviposition frequency of *Anolis carolinensis*. *Copeia* 1985:259–262.

ANDREWS, R. M., AND A. S. RAND. 1974. Reproductive effort in anoline lizards. *Ecology* 55:1317–1327.

ANDREWS, R. M., AND O. J. SEXTON. 1981. Water relations of the eggs of *Anolis auratus* and *Anolis limifrons*. *Ecology* 62:556–562.

ANDREWS, R. M., A. S. RAND, AND S. GUERRERO. 1983. Seasonal and spatial variation in the annual cycle of a tropical lizard. In G. J. Rhodin and K. Miyata (eds.), *Advances in Herpetology and Evolutionary Biology—Essays in Honor of Ernest E. Williams*, pp. 441–454. Museum of Comparative Zoology (Harvard Univ.), Cambridge, MA.

BALLINGER, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in lizard. *Ecology* 58:628–635.

CORN, M. J. 1981. Ecological Separation of *Anolis* Lizards in a Costa Rican Rain Forest. Unpubl. Ph.D. diss., Univ. of Florida, Gainesville.

FITCH, H. S. 1970. Reproductive cycles in lizards and snakes. Museum of Natural History, Univ. of Kansas, Miscellaneous Publications 52:1–247.

———. 1975. Sympatry and relationships in Costa Rican anoles. *Occasional Papers of the Museum of Natural History, Univ. of Kansas* 40:1–60.

———. 1982. Reproductive cycles in tropical reptiles. *Occasional Papers of the Museum of Natural History, Univ. of Kansas* 96:1–53.

FITCH, H. S., AND R. A. SEIGEL. 1984. Ecological and taxonomic notes on Nicaraguan anoles. *Milwaukee Public Museum Contributions in Biology and Geology* 57:1–12.

GORDON, R. E. 1956. The biology and biogeography of *Anolis carolinensis* Voigt. Doctoral Dissertation Series, Pub. No: 20, 303. Univ. Microfilms, Ann Arbor, MI.

GUYER, C. 1988a. Food supplementation in a tropical mainland anole, *Norops humilis*: demographic effects. *Ecology* 69:350–361.

———. 1988b. Food supplementation in a tropical mainland anole, *Norops humilis*: effects on individuals. *Ecology* 69:362–369.

HUEY, R. B., E. R. PIANKA, AND L. J. VITT. 2001. How often do most lizards “run on empty”? *Ecology* 82:1–7.

JANZEN, D. H. 1983. *Costa Rican Natural History*. Univ. of Chicago Press, Chicago.

JENSSEN, T. A. 1970. Ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). *Journal of Herpetology* 4:1–38.

MARITZ, M. F., AND R. M. DOUGLAS. 1994. Shape quantization and the estimation of volume and surface area of reptile eggs. *Journal of Herpetology* 28:281–291.

MITTERMEIER, R. A., N. MYERS, AND C. G. MITTERMEIER. 2000. Hotspots: Earth’s Biologically Richest and Most Endangered Terrestrial Ecoregions. CEMEX, Conservation International.

- PIANKA, E. R. 1973. 1975. Niche relations of desert lizards. In M. Cody and J. Diamond (eds.), *Ecology and Evolution of Communities*, pp. 292–314. Harvard Univ. Press, Cambridge, MA.
- RAMIREZ-BAUTISTA, A., AND L. J. VITT. 1997. Reproduction in the lizard *Anolis nebulosus* (Polychrotidae) from the Pacific coast of México. *Herpetologica* 53:423–431.
- RAND, A. S., AND C. W. MYERS. 1990. The herpetofauna of Barro Colorado Island, Panama: an ecological summary. In A. H. Gentry (ed.), *Four Neotropical Rainforests*, pp. 386–409. Yale Univ. Press, New Haven, CT.
- RUBY, D. E. 1981. Phenotypic correlates of male reproductive success in the lizard, *Sceloporus jarrovi*. In R. D. Alexander and D. W. Tinkle (ed.), *Natural Selection and Social Behavior*, pp. 96–107. Chiron Press, New York.
- SAVAGE, J. M. 2002. The amphibians and reptiles of Costa Rica: a herpetofauna between two continents, between two seas. Univ. of Chicago Press, Chicago.
- SCOTT, N. J., J. M. SAVAGE, AND C. C. ROBINSON. 1983. Checklist of reptiles and amphibians. In D. H. Janzen (ed.), *Costa Rican Natural History*, pp. 367–374. Univ. of Chicago Press, Chicago.
- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- SMITH, H. M., G. SINELNICK, J. D. FAWCETT, AND R. E. JONES. 1973. A survey of the chronology of ovulation in anoline lizard genera. *Transactions of the Kansas Academy of Science* 75:107–120.
- STAMPS, J. A. 1983. Sexual selection, sexual dimorphism and territoriality. In R. B. Huey and C. Gans (eds.), *Lizard Ecology: Studies of a Model Organism*, pp. 169–204. Harvard Univ. Press, Cambridge, MA.
- TINKLE, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. *American Naturalist* 103:501–516.
- TINKLE, D. W., H. M. WILBUR, AND S. G. TILLEY. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24:55–74.
- VITT, L. J., AND T. C. S. AVILA-PIRES. 1998. Ecology of two sympatric species of *Neusticurus* (Gymnophthalmidae) in the western Amazon of Brazil. *Copeia* 1998:570–582.
- VITT, L. J., AND J. D. CONGDON. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *American Naturalist* 112:595–608.
- VITT, L. J., AND H. J. PRICE. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38:237–255.
- VITT, L. J., AND P. A. ZANI. 1998. Prey use among sympatric lizard species in lowland rain forest of Nicaragua. *Journal of Tropical Ecology* 14:537–559.
- . 1996a. Ecology of the lizard *Ameiva festiva* (Teiidae) in southeastern Nicaragua. *Journal of Herpetology* 30:110–117.
- . 1996b. Ecology of the South American lizard *Norops chrysolepis* (Polychrotidae). *Copeia* 1996: 56–68.
- VITT, L. J., P. A. ZANI, AND R. D. DURTSCHKE. 1995. Ecology of the lizard *Norops oxylophus* (Polychrotidae) in lowland forest of southeastern Nicaragua. *Canadian Journal of Zoology* 73:1918–1927.
- VITT, L. J., P. A. ZANI, AND A. C. M. LIMA. 1997a. Heliotherms in tropical rainforest: the ecology of *Kentropyx calcarata* (Teiidae) and *Mabuya nigropunctata* (Scincidae) in the Cururuá-Una of Brazil. *Journal of Tropical Ecology* 13:199–220.
- VITT, L. J., P. A. ZANI, AND A. M. BARROS. 1997b. Ecological variation among populations of the gekkonid lizard *Gonatodes humeralis* in the Amazon Basin. *Copeia* 1997:32–43.
- VITT, L. J., P. A. ZANI, T. C. S. AVILA-PIRES, AND M. C. ESPÓSITO. 1998. Geographical ecology of the gymnophthalmid lizard *Neusticurus ecleopus* in the Amazon rain forest. *Canadian Journal of Zoology* 76:1671–1680.
- VITT, L. J., R. A. SOUZA, S. S. SARTORIUS, T. C. S. AVILA-PIRES, AND M. C. ESPÓSITO. 2000. Comparative ecology of sympatric *Gonatodes* (Sauria: Gekkonidae) in the western Amazon of Brazil. *Copeia* 2000:83–95.
- VITT, L. J., S. S. SARTORIUS, T. C. S. AVILA-PIRES, AND M. C. ESPÓSITO. 2001. Life on the leaf litter: the ecology of *Anolis nitens tandai* in the Brazilian Amazon. *Copeia* 2001:401–412.
- VITT, L. J., T. C. S. AVILA-PIRES, P. A. ZANI, AND M. C. ESPÓSITO. 2002. Life in shade: the ecology of *Anolis trachyderma* (Squamata: Polychrotidae) in Amazonian Ecuador and Brazil, with comparisons to ecologically similar anoles. *Copeia* 2002:275–286.
- VITT, L. J., T. C. S. AVILA-PIRES, M. C. ESPÓSITO, S. S. SARTORIUS, AND P. A. ZANI. 2003a. Sharing Amazon rainforest trees: ecology of *Anolis punctatus* and *A. transversalis* (Squamata: Polychrotidae). *Journal of Herpetology* 37:48–57.
- VITT, L. J., T. C. S. AVILA-PIRES, P. A. ZANI, S. SARTORIUS AND M. C. ESPÓSITO. 2003b. Life above ground: ecology of *Anolis fuscoauratus* in the Amazon Rainforest with comparisons to its nearest relatives. *Canadian Journal of Zoology* 81:142–156.
- VITT, L. J., E. R. PIANKA, W. E. COOPER JR., AND K. SCHWENK. 2003c. History and the global ecology of squamate reptiles. *American Naturalist* 162:44–60.

Accepted: 3 October 2004.